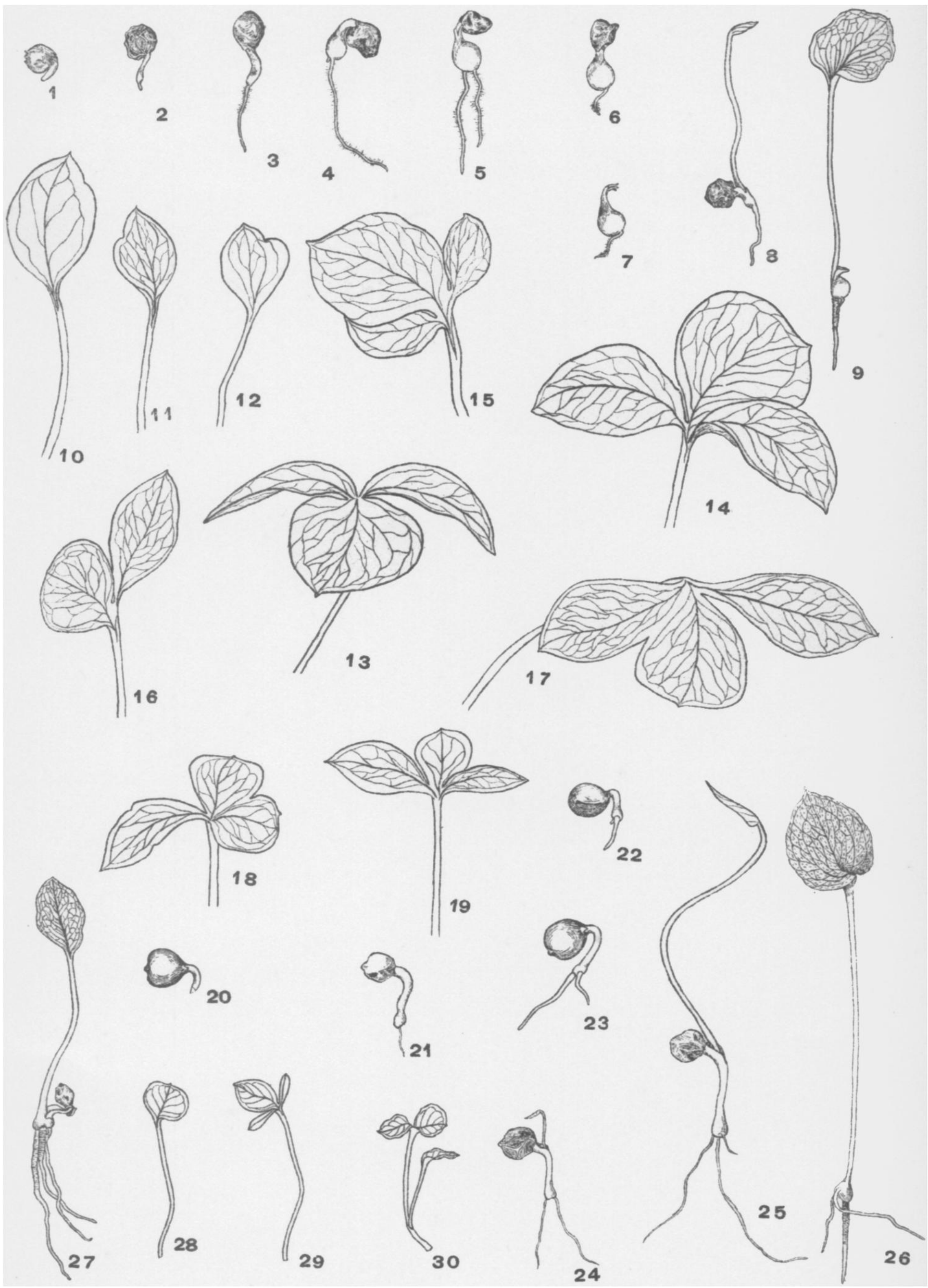

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Seeds and Seedlings of Arisaema triphyllum and Arisaema Dracontium

By Rosina J. Rennert

(Plate 3)

Some interesting facts in the germination of the seeds of *Arisaema Dracontium* have been recently described by Dr. MacDougal, and the author has devoted a greater part of the last year to the comparative study of the morphology and physiology of the seedlings of this species and of *A. triphyllum*. Some attention was also given to seedlings of a hybrid between the two species and those of *A. flavum* from Sikkim, India.

It was previously found by Dr. MacDougal that the plumule of *A. Dracontium* emerges from the cotyledonary sheath only in a small proportion of the seedlings, and that only a few of those emerging exhibited a development sufficient to carry the lamina of the first leaf up into the air and unfold it to the light.*

According to Braun, the closely related species *Arum maculatum* displays a similar behavior. He says "So spielt auch an der Keimpflanze die Niederblattbildung eine grossere Rolle, als bei *Calla*, in dem nach Irmisch auf dem Cotyledon zunachst mehrere unterirdische vegetirende Niederblatte folgen bevor ein Laubblatt, und zwar erst im zweiten Jahre zum Vorschė in kommt."† This statement seems to have escaped the notice of Scott and Sargant who have recently made an extended study of these seedlings.‡

The seedlings of *A. triphyllum*, on the other hand, send up a plumule as soon as the hypocotyl is firmly established in the soil, while the hybrid between *A. Dracontium* and *A. triphyllum* displays a curiously intermediate type of germination. The hypo-

* MacDougal, D. T. Seedlings of *Arisaema*. Torreya, **1** : 2. 1901.

† Braun. Ueber das Vorkommen mehere Hullblätter am Kolben von *Arum maculatum* L., *Calla palustris*, und *Richardia Africana* Kth. Verh. bot. Ver. Brandenburg, **1** : 94. 1859.

‡ Scott and Sargant. On the Development of *Arum maculatum* from the Seed. Annals Bot. **12** : 399. 1898.

cotyl, in this case, increases in size at first without sending up a plumule, and it is only after the seedling has exhausted the entire food supply of the endosperm and has separated from the seed that the plumule appears.

Like *A. triphyllum* the Indian species, *A. flavum*, follows the normal type of germination, and its plumule arises shortly after the hypocotyl emerges from the seed. The seedling is only about one half the size of that of *A. triphyllum*.

As the general structure of the seedling of *A. triphyllum* resembles most closely that displayed by *A. Dracontium*, this species was chosen as a basis for comparison in the study of the curious variations of *A. Dracontium*.

The fruits of *A. Dracontium* and *A. triphyllum* are very similar. In both the scarlet berries, which have a sweetish, slightly acrid taste, are closely crowded upon the spadix. The berries of *A. Dracontium* are larger and fleshier than those of *A. triphyllum* and contain from three to six seeds, while those of *A. triphyllum* are one- or three-seeded. In shape the seeds of both are somewhat ovoid. At the hilum, the seed of *A. Dracontium* is generally puckered into two or three ridges and the short stalk of the funiculus is conspicuous, while in *A. triphyllum* the seed is flattened in the hilar region, but also bears a prominent funiculus. Elsewhere the seeds are well rounded, except when flattened by the pressure of other seeds in the same berry. Both seeds bear a rudimentary aril which consists of a small disc-shaped fleshy mass situated immediately inside the coats at the hilar end of the seed, and extending as a core down the funiculus. The average size of the seeds of *A. Dracontium* is 3.5 mm. in transverse and 4.25 mm. in longitudinal diameter, while the average seed of *A. triphyllum* is 4 mm. in transverse and 3.5 mm. in longitudinal diameter, almost exactly reversing the proportions of *A. Dracontium*. When only a few are produced in a berry, the seeds of *A. Dracontium* are larger in both axes than those of *A. triphyllum*, which develop singly. When, however, a number of seeds mature in the same berry they develop in such a position as to exert a lateral pressure upon each other and in consequence the transverse diameter remains shorter. In these cases the seeds of *A. Dracontium* do not attain the size of even the smallest of *A. triphyllum*. On the whole, however, *A.*

Dracontium has the larger seed. The surface of both seeds is finely pitted and sometimes minute reddish spots are to be seen upon them. *A. triphyllum* has a yellowish color and *A. Dracontium* a reddish-yellow blush. This color is due to substances in the wall of the inner coat of the seed, as the testa is translucent.

In the general microscopic structure the seeds present only slight dissimilarities. The outermost row of cells in the testa of both species are brick-shaped and are set close together with their long axes at right angles to the radius of the seed. In both the walls of this outer row of cells are mucilaginous, swelling greatly when they come in contact with water. In *A. Dracontium* they are slightly larger and their outer walls are considerably thicker. A cuticle covers this row of cells in both species. Some of the cells below the outer row of the testa contain tannin, others are filled with mucilage in which raphide cells are imbedded, still others have a red coloring matter within them. It is to these latter cells that the dotted appearance sometimes noted on the seeds is due. The tegmen consists of three rows of tabular cells with very thick mucilaginous walls. In *A. Dracontium* these walls are orange-colored, and in *A. triphyllum* yellowish in color and so serve to give each seed its distinctive appearance. There is a cutinized lamella on either side of the tegmen cells.

The seeds of both plants are orthotropous and the embryo is imbedded in an abundant endosperm. In *A. triphyllum* the endosperm appears entirely homogeneous to the naked eye, while in *A. Dracontium* there is a horny layer next the seed coats. Upon microscopic examination, however, but slight differences are evident. The outer portion of the endosperm of *A. Dracontium* consists of 3 to 5 rows of cubical aleurone cells with walls capable of great swelling in water. These cells contain granular proteid globules, a single crystalloid, and also a small amount of fat. The aleurone cells of *A. triphyllum* are of exactly the same character, but are generally only from two to four rows deep, and also a trifle smaller. Within the layers of aleurone cells, making up by far the greater part of the endosperm, are large starch-bearing cells which have thin cellulose walls. Numerous crystalloids are imbedded in the starch of these cells. These crystalloids are slightly more numerous in the seeds of *A. Dracontium.* In both cases, however,

they are very abundant near the aleurone cells and become scarcer toward the embryo at the center of the endosperm. It will be seen that the only difference between the two seeds lies in the size of the cells which compose the aleurone layer and the seed coats. It follows from the greater size of the seed of *A. Dracontium* that this species has a food supply slightly greater than that of *A. triphyllum*.

Both resting embryos occupy a position near the base of the seed. In fact the aleurone cells near the micropyle are obliterated and the base of the hypocotyl of each embryo is close to the tegmen at this point. The cavity in which the embryo lies, but does not entirely fill, corresponds in general shape to that of the embryo and extends as an axis from the micropyle to the hilar region through the center of the seed. Its sides are formed of starch-bearing cells, aleurone cells close to the cavity at the hilar end, while the tegmen bounds it at the opposite end as described above. The embryos are club-shaped and small in proportion to the amount of endosperm contained in the seeds. In *A. Dracontium* they are 2 mm. long and .75 mm. thick, while those of *A. triphyllum* are slightly larger, measuring 2.75 mm. in length and .5 to .875 mm. in thickness. In *A. triphyllum* three fourths of the length of the embryo consists of cotyledon, the remainder is taken up by the hypocotyl. This relation is different in *A. Dracontium*, for the cotyledon in this case bears a slightly greater proportion to the entire length of the embryo. A slight constriction marks the insertion of the cotyledon on the hypocotyl, and a very small protuberance at the base of the hypocotyl is the incipient radicle.

Five regions are already differentiated in the resting embryo of each species, the dermatogen, procambium, root cap, meristem and fundamental parenchyma. The dermatogen is continuous with the epithelial layer which covers the entire embryo and, at the slit for the emergence of the plumule in the cotyledonary tube, is deflected back to line the plumular cavity. In the plumule of *A. triphyllum* dermatogen is already clearly differentiated but in *A. Dracontium* it is not so evident. The dermatogen is composed of a single row of narrow cells with their long axis at right angles to the longitudinal axis of the embryo. They are filled with aleurone grains and each contains a crystalloid. The procambium

strands which foreshadow the bundles have already been laid down in the cotyledon, stem-bud and hypocotyl. Near the tip of the cotyledon the procambium strands branch and anastomose irregularly and therefore no definite number or arrangement of them can be determined, but at the base the number becomes constant and each strand occupies a regular position. The plan of arrangement in both species is similar. In cross section the strands mark out a crescent in which the largest is at the middle of the bow. In *A. triphyllum* which has regularly five strands, two lie on either side of the central ones, while the cotyledon of *A. Dracontium* shows the same arrangement of its five principal strands, but has in addition one or two smaller ones. When there are two, these extra strands occupy positions on either side of the large middle trace. When only one extra strand is retained, it invariably is at the right. In the tubular portion of the cotyledon, the largest strand is in the thickest part of the wall. The strands are composed of six or seven rows of narrow elongated cells which have their long axis four to six times the length of their radial, and parallel with the longitudinal axis of the embryo. In the stem-bud, procambium strands have also been differentiated. In *A. Dracontium* the strands in the plumule are faint and there is some variation in the number of the procambial regions. They are never more numerous than three and at times only the pro-cambium of the future midrib has been laid down. In *A. triphyllum* five distinct procambium regions can be distinguished in the plumule. Procambium strands are also present in the hypocotyl and occupy fully one half of its entire diameter. They are continuous with the procambium of the stem-bud and form at the base of the hypocotyl the rudimentary root stele. At the base of the hypocotyl the root-cap may be distinguished, made up of several rows of rather large cells which stretch across its entire base and are continuous at the sides with the dermatogen of the embryo. In the outer rows the cells are empty. Meristem tissue is to be found at the stem-bud and at the base of the hypocotyl where the root takes its origin. These cells are very small and nearly isodiametric. Their nuclei are large and fill almost the entire cell. Parenchyma cells make up the rest of the embryo. They are two or three times the size of the epidermal cells and are packed with

starch. Scattered through the inner tissue are large cells filled with proteids in which a crystalloid also is embedded. These proteid cells are distributed through the tissues in those regions where the pro-cambium strands first make their appearance.

The embryos of the two species are similar in shape, position in the seed and general structure. *A. Dracontium* differs from *A. triphyllum* in four particulars: (1) Its size, (2) The proportion which the length of its cotyledon bears to its hypocotyl, (3) The number of procambium regions to be found in the cotyledon and (4) The state of differentiation of the procambium strands in the plumule. Here already the tendency in *A. Dracontium* to delay the development of the plumule is evident.

THE GERMINATION OF THE SEEDLINGS

In both species when water reaches the seeds the mucilaginous walls of the outer row of cells of the testa swell, while the cells below, pulled out by the swelling outer row and pushed out by the increase in size of the mucilaginous tegmen and the walls of the aleurone cells, separate and show an irregular alternation of large and small cells, which are, of course, empty. The seeds now increase considerably in size by the absorption of water, and the action of the moisture slowly reduces the outer row of the testa cells to a gelatinous film about the seeds. The mucilaginous tegmen is also soon dissolved, while all that remains of the seed coat is the inner part of the testa. The tannin in the vesicles contained within this becomes diffused through the whole of the cellulose coat and makes it more resistant to the disintegrating action of the soil. This part of the coat alone adheres to the seed until the last particle of endosperm is dissolved. The mucilaginous cells of the seed coat and the thick walls of the aleurone cells serve to increase the absorption of water, while the outer row of the testa is instrumental in bringing about the attachment of the seed to the soil.* The cellulose layer of the testa, impregnated with tannin, protects the endosperm during germination. When water reaches the embryo in the seed it swells and fills the cavity in which it lies, so that its epithelial cells are in contact at the sides with the starch

* Klebs. Beiträge zur Morphologie und Biologie der Keimung. Untersuch. a. d. Botan. Institut z. Tubingen. 1: 536. 1885.

cells of the endosperm. Here the diastase formed by the epithelium of the embryo can begin to act upon the stored starch of the seed and a proteolytic enzyme to dissolve the crystalloids. The starch of the endosperm is absorbed before the crystalloids, and when the cells in contact with the embryo have been emptied of their contents the cell walls are pushed back by the advancing growth of the cotyledon and the enzyme acts upon the contents of the cells next outside. The proteids of the aleurone cells do not become soluble until late in the history of the seedling. The cell walls of the endosperm do not seem to be acted upon by any enzyme, and are wholly intact until the seed separates from the seedling.

While the epithelial cells are secreting the enzymes, the cotyledon increases in length and by its elongation pushes the hypocotyl, bearing the stem-bud, through the seed coats at the micropyle. *A. Dracontium* requires fully a month longer than *A. triphyllum* for its hypocotyl to protrude. When the hypocotyl has wholly emerged from the seed it is directed down into the ground at right angles to the plane of the cotyledon, which is still in the seed. This is effected by means of a bend in the cotyledon at the place where it leaves the seed. This downward pull of the hypocotyl serves to tilt the seed up, and is sufficient when the seed has not been planted deep to break through the ground and bring the seed to the surface. In all cases it loosens the earth about the seedling, and so renders it easier for the pumule to make its way through the soil.

A great part of the cotyledon is confined within the seed during its entire development. The length which the cotyledons attain varies in both species, but those of *A. Dracontium* are on the average shorter than those of *A. triphyllum*. The average length of the *A. Dracontium* cotyledons outside of the seed is 3 mm., while those of *A. triphyllum* reach an average length of 7 mm. The number of the cells in the cotyledon is not increased by its elongation, for its entire growth is due to the increase in size of the already existing cells. The epithelial cells, which in the resting embryo had their axis perpendicular to the longitudinal axis of the embryo, now in the region of the cotyledon have this relation completely changed. Their long axes are parallel with the longitudinal

axis of the embryo. The cells of the parenchyma have also taken on an elongated form. The only region in the cotyledon where new cells are added is that occupied by the procambium and fibrovascular bundles. Here the cell division is very active. Radial growth takes place only as the contents of the endosperm cells is absorbed. The shape, arrangement of cells and manner of elongating are exactly similar in the cotyledons of *A. Dracontium* and *A. triphyllum*. It is only in the fibrovascular system that any difference between them has been discovered. Here in both cases, as in the procambium strands in the embryo, the bundles near the tip, branch and anastomose so that their distribution is irregular. At the base, however, the number of bundles is constant. *A. Dracontium* as a rule possesses six bundles: one of these strands is very weak and occupies the same position as the sixth procambium strand in the cotyledon, *i. e.*, at the right of the largest central bundle. The left hand strand which corresponds to the seventh in the resting embryo disappears before the cotyledon has proceeded very far with its development. The cotyledon of *A. triphyllum* has five bundles arranged as in the resting embryo. In a few instances chlorophyl has been found in that part of the cotyledon of *A. Dracontium* which protrudes from the seed both when the plumule was functional and when it was not. These cases, however, are uncommon.

Up to this point there is almost absolute identity in the germination of these two species: the only difference between them lies in the various sizes which the cotyledons attain. After this stage in the germination has been reached, however, various differences in the order of development of the organs become apparent.

The rudiments of all the structures of the mature corm are present in the hypocotyl of both *A. triphyllum* and *A. Dracontium* and the formation of the corm is brought about by the enlargement of the base of the hypocotyl and the laying down in it of the definitive tissues. In both it increases in bulk at least to a small extent before the first primary root is sent out. The hypocotol of *A. Dracontium* enlarges at a very much more rapid rate in the first stages of germination than does *A. triphyllum* and generally attains a considerable development before the root appears. A seedling of *A. Dracontium* with two roots each only 1 mm. in length

may have a corm 4 mm. in diameter while in a well-developed seedling of *A. triphyllum* with a strong system of roots and a plumule well grown, the corm may be only 1.75 mm. in diameter. The enlargement of the corm of *A. triphyllum* becomes marked only after the leaf is well established as a photosynthetic organ. In those seedlings of *A. Dracontium* in which the plumule does not become functional the corm, when its growth is completed, averages 4.5 mm. in diameter. When, however, the seedling has a functionating leaf the corm may attain a diameter of 6 mm. The corm of *A. triphyllum* may have a diameter of 5.75 mm. at the end of the season, but in many cases it is much less.

The enlargement of the hypocotyl is due to the increase both in size and number of its cells. As its growth is rather radial than longitudinal, the epithelial cells become isodiametric in shape. The storage cells increase in size and in number in all directions and so maintain the same relative dimensions. The starch grains contained in these cells are several times as large as those of the endosperm of the seed. The procambium cells of the hypocotyl are very active, dividing both in their longitudinal and transverse diameters and the fibro-vascular system soon becomes differentiated. Raphide cells are numerous in the corm and in all parts of the seedlings of the two species. As the corm enlarges, a layer of periderm arises on the outside, from which are cut off tangentially five or six rows of empty flattened cells. In addition to the protection they afford the corm, these periderm cells are instrumental in effecting a separation between the cotyledon and the corm, after the food supply of the endosperm has been absorbed. They grow between the cotyledon and the corm and separate the two by proliferating cells from their surface. In several instances chlorophyl has been formed in the two or three rows directly beneath the layers of periderm. The only difference in the development of the corm of the two species lies in the earlier enlargement of the hypocotyl of *A. Dracontium* and the greater average size of its completed corms.

The time at which the roots of *A. Dracontium* appear varies markedly. In some cases the hypocotyl enlarges greatly, becoming, as was described above, about 3 mm. in diameter before the first root arises. In other instances the roots are developed as

soon as the hypocotyl has found its way into the ground. Seedlings of *A. Dracontium* vary greatly also in the number and kinds of roots which they send forth. Those with the most well developed system have two primary roots from the base of the hypocotyl and later a thick root arising adventitiously from the the nodes. This secondary root, becomes contractile and transversely ridged for part of its length. One of the primary roots also often becomes contractile and helps to draw the corm deeper in the ground. A secondary root, however, is developed only in those seedlings which also send up a plumule and a few even of these have none. The seedlings in which the plumule has not started into activity have as a rule two primary roots, one of which becomes thickened and assumes the function of contraction. In some cases neither of the primary roots is contractile and in others only one short thin root is produced. A direct correlation between leaf and root development is here evident. Variations in the structure as well as the number of the roots occur. The contractile roots which are for the most part simple have been observed occasionally to be branched. In another instance (the single case in which two contractile roots occurred in the lot of *A. Dracontium* seedlings observed) two contractile roots were fused for part of their length. The root system of *A. triphyllum* is very much better developed than is that of *A. Dracontium*, for the roots are both longer and more numerous. The seedlings have always two and often three primary roots which reach a length of 5 cm. and in addition after the seedling is well under way, three thick adventitious roots appear, budding from the nodes. These roots are contractile and show the same transverse ridges as the contractile roots of *A. Dracontium.* In some cases they pull the hypocotyl down as much as 2 or 3 cm. below the level at which it germinated. After the secondary roots become firmly established, the primary roots grow no more and the greater part of the entire root function is discharged by the contractile roots which bear root hairs near their tips and become about 7 cm. long.

The only difference in microscopic structure between the contractile, secondary and primary roots consists in the greater radial elongation of the cells of the inner cortex of the contractile roots. In *A. Dracontium* the root stele of the primary root shows a diarch

structure and the secondary roots are tetrach as a rule. Some, however, have been observed to be triarch ; in *A. triphyllum* both primary and contractile roots are triarch. After the contraction of the roots the outer cortex cells are very much strained and twisted, but the radial elongation of the inner cells protects the stele from any distortion. The roots of *A. Dracontium* are more variable in all respects than those of *A. triphyllum*.

The stem-bud of *A. Dracontium* and *A. triphyllum* have the same structure in the resting embryo, with the exception that the procambium stands in the bud leaves have reached a more advanced stage of differentiation in *A. triphyllum*. During the first season's growth, however, the structure of the bud in the two species has an entirely different history. Like the roots the plumules of the *A. Dracontium* seedlings vary greatly in the state of development which they attain. As a rule the plumule of '*A. Dracontinm* develops to at least a small degree after germination, forming a lamina and a short petiole which although it may break through the cotyledonary sheath, yet rarely reaches the air and is often represented only by a rudiment 2 mm. in length remaining permanently enclosed by the cotyledon and enwrapping in its turn the stem-bud of the next year. This undeveloped plumule is cut off at the end of the season by the formation of a periderm between it and the corm in the same way as the cotylendon is separated from the corm. About 10 per cent. of the seedlings of *A. Dracontium* produce functional plumules. They appear at different stages during the growth of the corm, generally when it has already attained a considerable size and in some cases only after the seedling has entirely separated from the seed. Its method of emergence from its enclosing cotyledon is exactly the same as that of *A. triphyllum* which produces a plumule normally. As soon as the root has secured a firm hold on the soil and the hypocotyl is only slightly enlarged, the plumule with its blade recurved parallel to the petiole and rolled in at the margin breaks through the tubular part of the enclosing cotyledon through a longitudinal slit which is already present in the resting embryo. The plumule becomes green rapidly while the petiole at the base of the lamina straightens out and the folded blade unrolls and grows larger.

The functional plumules of *A. Dracontium* exhibit a tendency toward degeneration. A comparison of the plumules of the two species will well demonstrate the particular instances. The fully grown leaves of *A. triphyllum* are ovate, the largest being 36 mm. in length and 30 mm. in width, while the smaller are 25 mm. by 13 mm. The functional leaves of *A. Dracontium* vary greatly in the shape and size of the lamina and in the length of the petiole. In outline they range from broadly elliptical to nearly circular and all bear a mucronate point at the tip as does *A. triphyllum.* The largest leaves of *A. Dracontium* are about 25 mm. in length by 22 mm. in width, but the greater number are smaller, some being only 6 mm. by 3 mm. The margin of nearly all leaves of *A. triphyllum* are very finely serrulate; while some leaves of *A. Dracontium* display a tendency to serrulation, more often they are entire. The upper surface of the *A. triphyllum* leaf is covered with faint whitish lines; this appearance is due to the presence of elongated raphide cells in the mesophyll directly beneath the epidermis. *A. Dracontium* has numerous raphide cells in the mesophyll but they are not so large as those of *A. triphyllum* and cannot be distinguished without the aid of the microscope. The under surface of the leaves of *A. triphyllum* is covered with a waxy bloom and the upper surface also shows some wax. In *A. Dracontium* the wax is very much thinner on the under surface and barely discernible on the upper. As a consequence the leaf of *A. Dracontium* wilts very quickly after being removed from the plant. The development of stomata on both leaves is about the same. The leaves of both species are pinnately net-veined. In *A. triphyllum* one pair of the lateral branches is more strongly marked than the others, foreshadowing distinctly the plan of the mature trifoliolate leaf. In *A. Dracontium* the plan of venation is more generalized. The lateral veins have all equal value and are neither so well marked as some nor so faint as other lateral veins of the leaf of *A. triphyllum.* The mesophyll of the *A. Dracontium* leaf is not so well developed nor so well supplied with chlorophyll as is that of *A. triphyllum.* Those plumules of *A. Dracontium* which become assimilatory organs are functional for a shorter period than those of *A. triphyllum,* for they wither upon the plant much sooner. Those of longest duration last not more than three months while some send up

a petiole only, the blade being shriveled before it expands. Monstrosities seem to be very frequent in the leaves of *A. Dracontium*, for instance, the displacement of the mucronate point from the tip to the middle of the under surface of the midrib or the multiplication of these points upon the under surface. The blade is also often lobed upon one side and in one instance both sides of the leaf showed this peculiarity.

The petioles of the leaves of both species are streaked with red, the color being most abundant near the base. The petiole of *A. Dracontium* is considerably shorter than *A. triphyllum* and the fibro-vascular system is weaker on the whole although some stems of *A. Dracontium* and *A. triphyllum* show scarcely any difference. In the arrangement of tissue within the stem there is exact similarity. The bundles are arranged to form an open cylinder generally, in *A. Dracontium*, three on each side of the largest bundle. Those stems which attain the greatest development may have in addition a bundle running through the center of this cylinder, while in *A. triphyllum* the fibro-vascular system may include still another bundle, completing the cylinder and making nine bundles in all.

The development of the buds goes on during the growth of the seedling. Each rudimentary leaf arises as a hollow elevation enclosing the next youngest. At the end of the season the stem-bud of *A. Dracontium* has four bracts which enwrap the bud at the center and *A. triphyllum* agrees exactly with this plan in structure. All but the innermost of these enclosing bud leaves remain as rudiments upon the corm protecting the bud. The fourth grows large enough to protect the leaf as it pushes through the soil the second year, but remains at its base as a membraneous sheath.

The second season all *A. Dracontium* corms, like those of *A. triphyllum*, produce one trifoliolate leaf enclosed at the base by a sheath which, in those cases where no plumule is produced, must be regarded as the first leaf sent up by the plant. The functional leaf of the second season is trifoliolate normally, but is subject to great variation, such as the whole or partial fusion of two of its lobes or the complete obliteration of one of them. Even when the leaf is regularly trifoliolate great variations occur in the shape of

the individual leaflets. In some, the side leaflets may be narrowly lanceolate while others may approach an elliptical shape. The mid leaflet is generally broader than the lateral ones, but here too a variety of forms may occur. At the end of the second season's growth there is still a slight difference in the size of the corms of those plants of *A. Dracontium* which have borne a plumule the first year and those that have not. The root systems are, however, similar; six adventitious roots are developed in each. Except in the retarded development of its plumule, the development of the stem-bud of *A. Dracontium* agrees with that shown by *A. triphyllum*. The repression of the plumule does not seem to be correlated with any variations in the stem-bud of the second season, since variations of leaf form occur as frequently in second-year plants which produced a functional plumule the first season.

The principal differences between the seedlings of *A. Dracontium* and *A. triphyllum* consist not only in the reduction and variability of the roots, the variation and repression of the plumule on the part of *A. Dracontium*, but also in the precocious enlargement of the corm. This difference arises as soon as germination starts; in *A. Dracontium* the foodstuff of the endosperm is employed directly to build up the hypocotyl at the expense of the development of root and plumule. In *A. triphyllum*, however, as soon as the hypocotyl breaks through the seed coats, the roots are sent out and attain some development at once, the plumule then appears, and in normal cases it is only after this assimilatory organ is well established and the seedling has separated from the seed that the hypocotyl begins to enlarge. In *A. triphyllum* the endosperm furnishes the material which is necessary to bring the root and plumule to an advanced stage of development, and the food material for the hypocotyl is supplied by the assimilation of the plumule. The early enlargement of the corm and the repression of the plumule can scarcely be held to be due to a pathological condition of the seed or to an unfavorable environment, as the seeds planted were perfectly sound and the plumules in the embryos of those from the same lot which were examined showed no evidence of the attacks of parasites or any abnormality, while the conditions under which the plants were grown corresponded to the normal environment of these plants as was well demonstrated by

the vigorous growth of *A. triphyllum* which was subjected to the same conditions.

On the other hand the small proportion of functional plumules developed by seedlings of *A. Dracontium* and, in the cases in which a leaf was produced, the great variations in shape, the small size, the generalized form and venation, the delicacy of the lamina and the weak development of wax upon it, the shortness of the petiole and the frequent appearance of monstrosities, all are indications of degeneration and lead to the conclusion that this seedling is losing its power to produce a normal assimilating plumule. This conclusion is borne out by an examination of the internal structure. The petioles of the smaller leaves of *A. triphyllum* show the same arrangement of fibrovascular bundles as the largest of *A. Dracontium* and a series of increasingly smaller plumules which may easily be obtained from a number of seedlings shows a successively more generalized development of fibrovascular system until in the least developed system it becomes reduced to a mere rudiment. The highly organized fibrovascular system of the hypocotyl, which is of very little service to the seedling without a plumule and only a weakly developed root system, is still retained and bears evidence that the present type of seedling which brings a plumule to various stages of imperfect development may be a degeneration from a condition like that of the seedlings of *A. triphyllum* with a plumule normally functional.

So far as has been observed this type of germination is of no benefit to the seedlings. It does not seem to enable the corms to escape from the danger which they incur of being torn up by animals, for the development of the seedling without a strong root system of course precludes any great downward pull upon the corm by the contraction of its roots. Those plants of *A. Dracontium* which develop a leaf and correlated with this a stronger root system have invariably been found buried deeper than the plants whose plumule is not functional, for although in the plumuleless seedlings there is no upwardly directed force to bring the corm near the surface such as the plumule exerts in forcing its way through the ground yet on account of the weakness of the root system the tendency is such as to keep the corms very near the depth at which the seeds germinated. The repres-

sion of a plumule, of course, prevents the destruction of young seedlings by grazing animals; but the well-developed plumule contains enough raphide cells to protect it from attacks of this kind and the advantage which the plants enjoy in this respect is largely over-balanced by positive disadvantages. This variation, therefore, can scarcely have been perpetuated because of the advantage as a means of defense which plumuleless seedlings possess. As far as can be discovered at present this variation is of no benefit to the plant but, on the contrary, there are great disadvantages in this method of germination, which tend to throw the plant entirely upon the food supply of the parent form for another season.

The germination of *A. Dracontium* consists essentially in the conversion of the hypocotyl of the embryo into the corm of the seedling by the transfer of the food material contained in the endosperm. In some aroids,* this resorption of the endosperm and conversion of the base of the hypocotyl into a corm takes place before the embryo leaves the seed; that is to say, the development of the seed is not completed until a bulbiform embryo with true fibro-vascular bundles and no trace of cotyledon has been formed. An example of this type is *Spathyema foetida*. When the seed of this plant germinates the stem-bud pushes out of the micropyle and breaks through the ground first; later adventitious roots spring from the nodes. No primary root is produced. It will be seen that the only difference between the germination of this seed and the sprouting of the first year's corm of *A. Dracontium* is the fact that in the former case the seed coats which surround the bulbiform embryo must be penetrated by the stem-bud. If the corm formation of the seedling of *A. Dracontium* took place within the seed coats (and this could be brought about simply by the arrest of the elongation of the cotyledon) the two cases would be exactly similar. In fact the cotyledon of *A. Dracontium* is varying in just this direction, for it often displays a tendency to be shorter than the cotyledon of *A. triphyllum* as has been pointed out above. The delay in germination at first, moreover, may be another indication of a tendency to carry on the entire development of the corm within the seed.

* Engler. Monographiae Phanerogamarum, Araceae, II : 34.

Owing to the lack of time and material the developmeut of the corm of *Spathyema* within the seed could not be traced but an examination of the literature of the subject brought out the fact that many aroids manifest a tendency to carry on the development of the plant as far as possible before actual germination, *i. e.*, emergence from the seed and development of assimilatory organs occurs.*

SUMMARY

The seeds of the two species present only a few unimportant differences in shape. In histological structure they are similar. The embryos are comparatively small and are imbedded in a copious farinaceous endosperm. The only essential distinction between them consists in the slightly greater amount of food material in the seed of *A. Dracontium*, the extra procambium strand of its cotyledon and the weaker development of procambium in the plumule of its resting embryo. The first stages of the germination of the two seeds are of the same character and consist in the emergence of the hypocotyl and stem-bud from the seed coats at the micropyle, by means of the elongation of the cotyledon.

As the development of the seedlings proceeds, the production of roots and a plumule takes precedence in *A. triphyllum* while in *A. Dracontium* the enlargement of the hypocotyl begins at once and the growth of the root and plumule is retarded. This precocious development of the corm often takes place to such a degree as to entirely inhibit the production of a functional plumule. The same differences between the two species in regard to the fibrovascular development is exhibited by the seedlings as is displayed by the resting embryo. The structure of the stem-bud which develops upon the corm during the first season's growth is absolutely the same in both species.

The seedling of *A. Dracontium* is diverging from what seems to be the normal type of germination in *Arisaema*, *i. e.*, the development of an assimilatory plumule and the production of a corm by means of the product of the photosynthetic activity of this organ, and is tending to produce a corm without the aid of a plumule by the direct transfer of the food material of the endosperm to the

* Engler. Monographiae Phanerogamarum. Araceae, **11** : 34, 35.
Griffith. Trans. Linn. Soc. **20** : 274–276. 1847.

hypocotyl. This type of germination does not seem to be due to a diseased condition of the seed or embryo or to an unfavorable environment nor does it appear to be advantageous to the young seedling. It might be suggested therefore that it is an expression of an inherent tendency in aroids to carry the young plantlet as far as possible in its development before an assimilatory organ is produced. If this conclusion be correct we have in *A. Dracontium* a transition stage between a seedling forming its corm outside of the seed coats with the aid of a plumule as in *A. triphyllum* and a corm formation within the seed coats at the expense of the endosperm as is the case with *Spathyema foetidus.*

Explanation of Plate 3

FIG. 1. Seedling of *A. Dracontium* showing hypocotyl just emerging from seed.

FIG. 2. Seedling of *A. Dracontium.* Hypocotyl has begun to enlarge, short root has appeared.

FIG. 3. Seedling of *A. Dracontium.* Root has elongated, root hairs have arisen.

FIG. 4. Seedling of *A. Dracontium.* Hypocotyl has enlarged greatly, first root has elongated, second root is just appearing.

FIG. 5. Seedling of *A. Dracontium.* Hypocotyl has attained full size of first year's corm.

FIG. 6. Seedling of *A. Dracontium.* Specimen in which the root system has been only slightly developed.

FIG. 7. First-year corm of *A. Dracontium.* Formation of periderm at base of cotyledon has separated corm from seed.

FIG. 8. Seedling of *A. Dracontium* which has produced plumule.

FIG. 9. Seedling of *A. Dracontium.* More advanced; note single contractile root, developed only in those cases where plumule is sent up.

FIGS 10, 11, 12. Variations in form of plumule in those seedlings of *A. Dracontium* which send up a leaf.

FIGS. 13, 14. Second-year leaves of *A. Dracontium* when a plumule had been developed by seedling.

FIGS. 15, 16, 17, 18, 19. First leaves produced by *A. Dracontium* corms which have been developed without the aid of a plumule.

FIG. 20. Seedling of *A. triphyllum.* Hypocotyl just emerging.

FIG. 21. Seedling of *A. triphyllum.* Cotyledon lengthened, hypocotyl has begun to enlarge, root has arisen.

FIG. 22. Seedling of *A. triphyllum.* Second root appearing.

FIG. 23. Seedling of *A. triphyllum.* Second root has increased in length.

FIG. 24. Seedling of *A. triphyllum.* Plumule has emerged from cotyledonary sheath.

FIG. 25. Seedling of *A. triphyllum.* Petiole of plumule has lengthened, a third root has appeared. Hypocotyl perceptibly enlarged.

FIG. 26. Seedling of *A. triphyllum.* Contractile root formed, plumule fully expanded.

FIG. 27. Seedling of *A. hybrida.* Plumule produced.

FIGS. 28, 29, 30. Variations in form of leaf produced second year by *A. hybrida.*